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Effects of elevated temperature and elevated CO_2 on soil nitrification and ammonia-oxidizing microbial communities in field-grown crop

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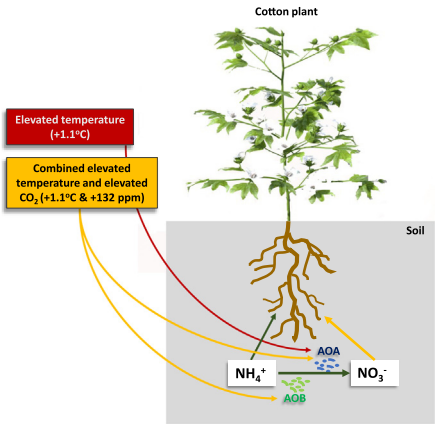
HIGHLIGHTS

- Soil nitrification and nitrifying communities respond differently to different climate treatments
- Combined elevated CO_2 and temperature increased nitrification rates and shifted community structure of nitrifying communities
- Crop developmental stage modified climate change impact on soil functions and microbial communities
- Changed nitrification rates and nitrifying communities can have consequences for farm productivity and environmental quality

GRAPHICAL ABSTRACT



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ABSTRACT

Rising global air temperature and atmospheric CO_2 are expected to have considerable effects on soil nutrient cycling and plant productivity. Soil nitrification controlled by ammonia-oxidizing bacteria and archaea (AOB and AOA) communities plays a key role in contributing to plant nitrogen (N) availability; however, response of soil nitrification and functional microbial communities to climate change and subsequent consequences for crop yields remain largely unknown. Cotton productivity is a function of temperature and N availability under well-watered conditions. In general, cotton growth responds positively to elevated CO_2, but simultaneous warming may offset benefits of rising CO_2. In this study, cotton was used as a model system to elucidate the short-term response of soil nitrification and ammonia-oxidizing communities to elevated temperature and elevated CO_2 using field-based environmentally-controlled chambers. Elevated temperature (ambient + 1.1 °C) altered the AOA community, while elevated temperature and elevated CO_2 (ambient + 132 ppm) significantly increased soil nitrification rate and shifted AOB and AOA communities, but these effects depended on cotton developmental stages. Ammonia-oxidizing community abundance and structure were statistically correlated with nitrifying activity. Our findings suggest that climate change will positively affect soil nitrifying communities, leading to an increase in process rates and subsequent N availability, which is directly linked to crop productivity.

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1. Introduction

Global climate models have projected a continuing increase in the global surface temperature as a result of increasing atmospheric CO_2 concentration (IPCC, 2013), potentially leading to considerable changes in agroecosystems in terms of primary productivity and nutrient cycling (Rosenzweig et al., 2007). Depending on the optimal temperature range of plants, warming may increase or decrease crop productivity (Trumbore, 1997; Rustad et al., 2001; Lobell and Field, 2007) while elevated CO_2 often enhances crop yields through higher photosynthesis and lower stomatal conductance, resulting in increased leaf-level water use efficiency (Kimball et al., 2002). Increasing temperature and CO_2 levels may affect soil moisture content (Chiew et al., 1995; Dijkstra et al., 2010), thereby possibly altering carbon (C) and N availability in soils (Gleeson et al., 2010; Barnard et al., 2013), which in turn can influence crop nutrition acquisition and yields.

Soil nutrient cycling is mainly driven by microbial communities to provide key nutrients for assimilation by plants (Singh et al., 2010). The nitrification process, consisting of two sequential steps including ammonia oxidation and nitrite oxidation (Bernhard, 2010), plays a crucial role in plant N availability, and N loss through gas emission and nitrate (NO_3) leaching (Zhalnina et al., 2012). Ammonia oxidation is a rate-limiting conversion controlled by AOB and AOA (Leininger et al., 2006). Bacterial ammonia oxidizers are mainly composed of *Beta-* and *Gamma-proteobacteria* (Purkhold et al., 2000) while ammonia-oxidizing archaea are affiliated within the phylum *Thaumarchaeota* (Könneke et al., 2005). Recent studies indicated that soil substrate ammonia (NH_4^+) is one of the key factors shaping functional and structural patterns of AOB and AOA because they obtain energy primarily via ammonia oxidation (Prosser and Nicol, 2012; He et al., 2012). In addition, soil moisture was the main driver for changes in AOB and AOA community structure and their function (Nguyen et al., 2018).

AOB and AOA cohabit most soils (Xia et al., 2011) and the ratio of AOB and AOA abundance ranges widely in soils (Jia and Conrad, 2009; Gubry-Rangin et al., 2010). Although AOA communities generally outnumber their counterpart AOB in various soils (Yao et al., 2013), their functional importance is not always equal to their numerical dominance (Di et al., 2009; Xia et al., 2011). For example, AOA were dominant in numbers, but AOB controlled nitrification rates in agricultural and grassland soils (Jia and Conrad, 2009; Sterngren et al., 2015). There has been increasing evidence indicating niche differentiation between AOB and AOA (Prosser and Nicol, 2008, 2012); however, their relative contribution to ammonia oxidation remains unclear particularly in agriculture fields. AOB were more functionally dominant in N-rich and alkaline soils (Shen et al., 2008), whereas AOA exhibited a higher affinity to ammonia and favoured low nutrient and acidic environments (Martens-Habbena et al., 2009; Yao et al., 2011). Therefore, differences in cellular, genomic, and physiological traits between AOB and AOA may lead to their distinct responses to climate change.

Temperature is an important factor influencing nitrification and nitrifying communities (Tourna et al., 2008; Fierer et al., 2009; Cao et al., 2013). Elevated temperature can directly or indirectly affect nitrification efficiency via influences on microbial metabolic activities (Hu et al., 2016; Karhu et al., 2014) or altering soil properties, including soil oxygen (O_2) level and substrate availability (Bradford et al., 2008; Bai et al., 2013). In contrast, elevated CO_2 may indirectly affect nitrification rates through plant-mediated impacts on soil properties (Singh et al., 2010). For example, increased root exudates and decreased plant stomatal conductance in elevated CO_2 may alter soil substrate availability and O_2 concentrations, respectively (Niboyet et al., 2010; Barnard et al., 2006). Alternatively, functional microbial communities may be changed in response to increasing CO_2 and temperature, leading to modification in fundamental physiologies driving process rates (Hu et al., 2016). However, it remains largely unknown whether, and how, nitrifying community structure and abundance are impacted, and subsequent consequences for nitrification rates in response to climate change in field conditions.

This study addresses the response of soil nitrification rates and ammonia-oxidizing communities to elevated temperature and elevated CO_2, and consequences for crop productivity, using cotton as a model system. The cotton industry is highly vulnerable to alterations in climate (Glover et al., 2008; Bange et al., 2016) because cotton strongly depends on temperature and N fertilization to maintain high productivity (Reddy et al., 1997; Weier, 1994). In the past few decades, Australian cotton crops have experienced substantially warmer maximum temperatures (Bureau of Meteorology). Although cotton crop yields may be positively responsive to elevated CO_2, concurrent high temperatures may at least partially negate CO_2 fertilization benefits (Reddy et al., 2005). In previous fully factorial glasshouse experiments, we demonstrated that C_e and T_e increased crop biomass and lint yields, which were constrained by the availability of soil nitrate (Osanai et al., 2017a, 2017b). Single factor experiments used to predict potential influences of future climate on crop productivity may be limited because the combined impacts of elevated CO_2 and temperature may be not additive. Field-based environmentally-controlled chambers were used to simulate future climates of elevated temperature and CO_2 for cotton grown under otherwise natural environmental conditions. We hypothesized that elevated temperature and elevated CO_2 will stimulate nitrification rates through influencing soil physicochemical properties or changes in functional microbial communities.

2. Materials and methods

2.1. Field site and cotton cultivar description

The field-based study was conducted at the Australian Cotton Research Institute (ACRI) in Narrabri, New South Wales (NSW), Australia. Narrabri (30.31°S, 149.78°E) is a semi-arid region with daily temperatures varying from 18 °C to 35 °C and annual rainfall of 644 mm, of which one-third falls in summer months (Bureau of Meteorology, NSW). High clay content soils (vertosols) with alkaline pH in the range of 7.5–8.0 are classified as Ug 5.25 according to the Northcote classification system (Northcote et al., 1975).

The CSIRO cotton cultivar Sicot 71 BRF was planted on ridges spaced 1 m apart separated by a furrow in which water was applied as furrow-flood irrigation. Typical farming practices including tillage and irrigation were applied. Cotton was nitrogen (N)-fertilized (anhydrous ammonia) at a rate of 180 kg N ha^{-1} prior to sowing (Braunack, 2013). In this study, cotton was sown in late summer (February 2015) and the field experiment was completed by the middle of autumn (April 2015).

2.2. Experimental design and soil sampling

Field-based environmentally-controlled chambers that controlled temperature and atmospheric CO_2 were used in this study. They were constructed of galvanized steel attached to a 1 cm thick transparent plastic segment at the front and back. The chambers were enclosed with two layers of transparent plastic sheets (100 μm thick) (clean), and were filled with air to provide greater temperature control during the experiment. The chambers ($4 \times 4 \times 3$ m) were portable and installed in the field when cotton plants were at the post-emergence stage (23 days after planting). Chambers were assembled outside the field and pulled into the field on their wheels along the furrow when cotton plants were at 23 DAP; once the chambers were fixed, the wheels were removed. Two chambers were set for each treatment ($n = 2$), including ambient atmospheric CO_2 and elevated temperature (C_aT_e); and elevated CO_2 and elevated temperature (C_eT_e). Two plots outside the chambers (C_aT_a) were used as field controls (Fig. S1).

An air conditioner unit was used to control air temperature inside the chambers, with the goal of achieving temperatures inside the chambers of 2–4 °C higher than ambient air temperature. CO_2 gas was

released into the chambers to maintain CO_2 concentration at ambient (400 ppm) and elevated (550 ppm) CO_2. The concentration of CO_2 inside each chamber was recorded using a LICOR-840A. The temperature and humidity conditions inside the chambers were measured by a Tiny Tag Ultra sensor (Gemini Data Loggers, West Sussex, UK) placed just above the canopy.

Plots were furrow irrigated three times during the experiment by adding irrigation water to the chambers through an underground pipe system. The first irrigation event was applied at 1 day after planting (DAP), the second event at 23 DAP, and the third event at 50 DAP. Each furrow irrigation event provided approximately 90–100 mm water. Drip irrigation systems were set up inside the chambers to ensure similar watering regimes in both the outside plots and inside the chambers. Drip irrigation was applied for plots inside the chambers at four different times: 37 DAP (5.4 mm water), 49 DAP (13.2 mm), 55 DAP (12 mm) and 62 DAP (11 mm), in order to match outside rainfall events.

Soil core samples (4 cm diameter and 10 cm deep) were collected four times during the growing season, representing different developmental stages of the cotton plants. The first sampling campaign was conducted before the chamber installation, corresponding to 15 DAP, when cotton plants were at the emergence stage. The other three sample collection campaigns were conducted 4 days after chamber installation (27 DAP), at the early squaring stage (41 DAP) and the early flowering stage (70 DAP). Five samples were collected each time for plots inside and outside the chambers. Soil samples were transferred to the Hawkesbury Institute for the Environment (HIE), Western Sydney University, NSW for analyses. Soil samples were passed through a 4 mm sieve to remove plant residue, then kept at 4 °C until analysis. Subsamples of soil were kept at −20 °C prior to molecular manipulations.

2.3. Soil physicochemical property analyses

Soil moisture content was determined using 5 grams (g) of fresh soil oven-dried at 105 °C for 24 hours (h). Soil pH was measured with a pH meter (SevenEasy pH, Metler Toledo, Switzerland) after a mixture of fresh soil and double deionized water (with a ratio of 1:5) was shaken for 1 h. Soil inorganic N including NH_4^+ and NO_3^- were extracted with 2 M potassium chloride (KCl) and then filtered by Whatman no.42 filter paper prior to analysing by using a SEAL AQ2 discrete analyser (SEAL Analytical Inc., USA). To determine soil total N and carbon (C), soil was oven-dried at 40 °C for 72 h and ground to a fine powder which was then analysed by LECO macro-CN analyser (LECO, USA).

2.4. Potential nitrification rate (PNR)

Soil PNR was determined based on the chlorate inhibition method (Kandeler and Böhm, 1996). Briefly, 5 g of fresh soil was mixed with a buffer containing 50 mg L^{-1} potassium chlorate ($KClO_3$) and 1 mM NH_4^+ while control samples were added only NH_4^+ and frozen at −20 °C for 5 h. The mixture was shaking-incubated at 25 °C for 5 h in dark. The suspension and control were then extracted with 2 M KCl and filtered by Whatman no.42 filter papers. Colour reagents including sulfonic acid ($NH_2C_6H_4SO_3H$) dissolved in 12% acetic acid (CH_3COOH) and naphthylamine dissolved in 20% acetic acid (CH_3COOH) were in turn added into the extracts (Hu et al., 2015). Subsequently, 200 μL of each solution was measured at 520 nm wavelength by a spectrophotometer microplate reader (Enspire® Multilable Reader, Perkin, Elmer, USA). Absorbance values were ultimately converted into N concentrations using a standard curve formulated from a series of sodium nitrite ($NaNO_2$) concentrations.

2.5. Ammonia-oxidizing community analyses

2.5.1. DNA extraction

Soil total genomic DNA was extracted using a MoBio PowerSoil DNA Isolation kit (MoBio Laboratories, Carlsbad, CA, USA) and FastPrep bead beating system at a speed of 5.5 m s^{-1} (Bio-101, Vista, CA, USA). After extraction, DNA quality and quantity were photometrically checked using a NanoDrop® ND-2000c UV–Vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). DNA samples were stored at −20 °C for further analyses.

2.5.2. Real-time PCR (qPCR)

Soil AOB and AOA abundance was determined via quantifying copy numbers of *amoA* genes using BioRad C1000 Touch thermal cycler CFX96 Real-Time system (Bio-Rad laboratory, USA). Two pairs of primers including amoA-1F/amoA-2R (GGGGTTTCTACTGGTGGT/CCCCTCKGSAAAGCCTTCTTC) (Rotthauwe et al., 1997) and CrenamoA23f/CrenamoA616r (ATGGTCTGGCTWAGACG/GCCATCCATATGTATGTCCA) (Tourna et al., 2008) target AOB and AOA *amoA* genes, respectively. Each reaction consists of 5 μL GoTaq® qPCR Master Mix (2×), 20 μM each primer, 0.1 μL CXR reference dye and 10 ng of template DNA. AOB *amoA* gene was amplified following conditions: an initial cycle of 95 °C for 10 min; 39 cycles of 94 °C for 45 s, 58 °C for 45 s, to 72 °C for 45 s; 1 cycle of 95 °C for 15 s, 60 °C for 30 s, to 95 °C for 15 s (Hallin et al., 2009). The PCR thermal condition to amplify AOA *amoA* gene was similar to that of AOB *amoA* gene, but annealing temperature was 55 °C (Hallin et al., 2009).

Standards for qPCR were constructed by cloning isolated AOA and AOB *amoA* genes into the pCR®4–TOPO vector (Invitrogen, Carlsbad, CA). A 10-fold serial dilution of plasmid was prepared to generate standard curves. Melt curve analyses were conducted following each assay to verify the specificity of the amplification products. PCR efficiencies for AOB and AOA assays were 88% and 95%, respectively.

2.5.3. Terminal restriction fragment length polymorphism (TRFLP)

Soil AOB and AOA *amoA* gene fragments were amplified using fluorescently labelled primers VIC-amoA-1F/amoA-2R and FAM-CrenamoA23f/CrenamoA616r, respectively. Each 25 μL reaction contained 5.5 mM $MgCl_2$, Taq DNA polymerase, 10 × NH_4 reaction buffer, 20 mM deoxynucleoside triphosphate (Bioline, Australia), 20 μM each primer (Sigma-Aldrich, Australia), 20 mg mL^{-1} BSA (NewEngland Biolabs, USA), and 10 ng DNA template. After denaturing the PCR mixture at 95 °C for 5 min, DNA template was amplified with 35 cycles of denaturing at 95 °C for 30 s, annealing at 56 °C for 30 s, and extension at 72 °C for 1 min, and finally extension at 72 °C for 10 min on a Dyad Peltier Thermal cycler (Biorad, Australia). PCR amplicons were then visualized on 1% (w/v) agarose gel under UV radiation to check for successful amplification.

PCR products were then purified using Wizard SV Gel and PCR clean-up System (Promega, San Luis Obispo, CA, USA). The quality and quantity of purified DNA were checked using NanoDrop® ND-2000c UV–Vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The ratio of $A_{260/280}$ and $A_{260/230}$ were in the range of 1.8–2.1 and 0.7–1.7, respectively. Purified DNA concentrations varied from 40 to 100 ng/μL.

Purified PCR products were then subjected to digestion using commercial restriction enzymes including *Msp*I and *Hpy*CH4V (New England BioLabs, USA) for AOB and AOA, respectively (Yao et al., 2011; Hu et al., 2015). A 10 μL reaction volume composed of 200 ng of DNA, 1 μL of 10× NEB buffer, 0.1 μL of BSA and 5 U of restriction enzyme was incubated at 37 °C for 3 h, followed by 95 °C for 10 min to deactivate the restriction enzymes. Terminal restriction fragments (TRFs) were resolved on an ABI PRISM 3500 Genetic Analyser (Applied Biosystems, CA, USA), using a geneScan 600-LIZ (Applied Biosystems) as internal size standard for each sample. Genemapper version 4.0 (Applied Biosystems) was used to analyse TRFLP profile. The output from Genemapper was then imported into T-REX software for further analysis (Culman et al., 2009), including quality control procedures by TRF alignment (clustering threshold = 0.9 pb), and noise filtering (peak area, standard deviation multiplier = 1). The relative abundance of TRFs was calculated based on peak height. TRFs with peak heights comprising <2% of the total

peak height were removed from downstream analyses to avoid artifacts (Hu et al., 2015).

2.6. Statistical analyses

Repeated measures ANOVA was applied to test whether there were significant effects of treatments and plant developmental stages on soil physicochemical properties, PNR, AOB and AOA *amoA* genes abundance. One-way ANOVA with Tukey's HSD test was used to compare means of different treatments at each plant developmental stage. Spearman's rank correlation analysis was conducted to examine relationships between variables. The *amoA* gene copy numbers were log-transformed prior to statistical analysis to meet normality assumptions. $P < 0.05$ was considered to be statistically significant. All these tests were manipulated in SPSS 22 (IBM, Armonk, NY, USA). Bray-Curtis dissimilarity matrices based on the relative abundance of AOA and AOB TRFs was visualized by principal coordinate analysis (PCO) using Primer v6 (PRIMER-E Ltd., Plymouth, UK), following PERMANOVA to examine significance of Bray-Curtis dissimilarity.

3. Results

3.1. Chamber effects and treatments

Average daily air temperature of ambient (C_aT_a) plots was 24.2 °C, while that of C_aT_e and C_eT_e treatments were 25.3 °C and 25.1 °C, respectively (Fig. 1). CO_2 concentration inside C_eT_e was 132 ppm higher than ambient plots (Fig. 1). There were statistically significant differences in daily average vapor pressure deficit (VPD) among treatments ($P = 0.011$), with VPD lower in the chambers compared to outside control (−13.75%; Fig. 1). Photosynthetically active radiation (PAR) in C_aT_e treatment (only chamber measured) was 23% lower than the outside control (Fig. 1).

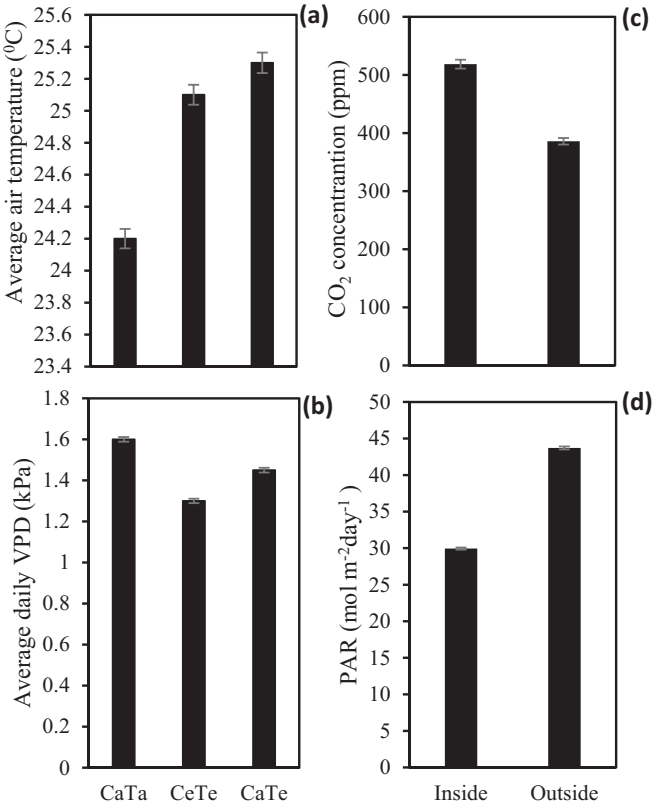

Fig. 1. Average daily temperature (a) and VPD (b) among climate treatments. Average CO_2 concentration (c) between C_eT_e and ambient plots. Average daily PAR between inside and outside C_aT_e chamber (d). Values represent mean ± SE ($n = 67$ for air temperature and average daily VPD; $n = 84$ for CO_2 level, and $n = 34$ for PAR) of each treatment. C_aT_a = ambient CO_2 and temperature, C_eT_e = elevated CO_2 and temperature, C_aT_e = ambient CO_2 and elevated temperature. VPD = daily average vapor pressure deficit, PAR = photosynthetically active radiation, SE = standard error.

3.2. Soil physicochemical properties in response to treatments

Overall, soil physicochemical properties (except total C) significantly changed with cotton growth stage ($P < 0.01$, Table 1). C_aT_e and C_eT_e significantly affected soil moisture and NO_3^- levels, respectively ($P = 0.001$ and $P < 0.001$, Table 1). At the early flowering stage of cotton plants (70 DAP), soil NO_3^- of C_eT_e was considerably lower than in C_aT_a and C_aT_e treatments (−25%, $P < 0.001$, Fig. 2), while soil moisture of C_aT_e treatment was approximately 2% lower than in C_eT_e and C_aT_a ($P = 0.027$, Fig. 2).

3.3. PNR and ammonia-oxidizing community abundance and structure in response to treatments

There was consistent impact of C_eT_e on PNR and AOB at all sampling times except the first sampling period. C_aT_e did not significantly affect soil PNR ($P = 0.063$, Table 1), whereas C_eT_e significantly impacted PNR ($P = 0.005$, Table 1). After 70 DAP, corresponding to the early flowering stage of cotton plants, soil PNR of C_eT_e increased by 6.7% when compared to PNR of C_aT_e and C_aT_a plots (Fig. 3). There was a similar trend for AOB abundance (Table 1). Particularly, AOB *amoA* gene abundance of C_eT_e treatment was significantly higher than C_aT_e and C_aT_a plots at 70 DAP (+7.8%, $P = 0.011$ and +15.5%, $P = 0.008$, Fig. 3). AOA *amoA* gene abundance also increased under C_aT_e and C_eT_e treatments, but only at 70 DAP (+4.9%, $P = 0.015$ and +8.3%, $P = 0.009$, respectively, Fig. 3).

Analysis of TRFLP profile indicated 4 and 8 different TRFs for AOB and AOA *amoA* genes, respectively (Fig. 4). TRF-55, 149 and 251 were dominant TRFs of AOB community while AOA community had dominant TRF-74, 243 and 251. In C_aT_e and C_aT_a plots, AOB community marginally changed with crop growth stage. In contrast, in C_eT_e, the relative abundance of TRF-149 and 251 significantly increased ($P < 0.001$), while that of TRF-55 significantly decreased ($P = 0.003$) at the early flowering stage (70 DAP). In the AOA community, the relative abundance of TRF-54 and 91 significantly increased ($P < 0.001$ and $P = 0.009$, respectively), whereas the relative abundance of TRF-74 significantly decreased, compared to C_aT_e and C_eT_e treatments at the early flowering stage ($P = 0.01$).

The phylogenetic affiliation of some TRFs could be assigned by searching identical TRFs from the study by Hu et al., (2015). AOB TRF-149 and 229 were placed within the *Nitrosospira* cluster. AOA TRF-74, 150 and 212 belonged to the *Nitrososphaera* cluster whereas AOA TRF-54 and 198 were in the *Nitrosopumilus* and the *Nitrosotalea* clusters, respectively (Table S1). These phylogenetic assignments combined with relative abundance of TRFs generated from TRFLP profile indicated that *Nitrosospira* significantly responded to C_eT_e, while phylotypes of *Nitrosopumilus* were significantly affected by both C_aT_e and C_eT_e.

PCO analysis explained 94.6% and 90.1% of variation (two axes) in AOB and AOA community structure, respectively (Fig. 4). C_eT_e treatment significantly affected AOB community structure as a function of crop growth stage (PERMANOVA, $P = 0.001$), while both C_aT_e and C_eT_e treatments had significant effects on AOA community structure as a function of crop development (PERMANOVA, $P = 0.001$).

3.4. Drivers of soil ammonia oxidation process

Spearman's rank correlation analysis indicated statistically positive significant correlations between AOB, AOA abundances and PNR ($r_s = 0.810$, $P < 0.001$ and $r_s = 0.507$, $P < 0.001$, respectively, Table 2). Soil pH was positively correlated with AOB abundance and

Table 1
Repeated measures ANOVA for effects of climate factors and cotton developmental stages on soil physicochemical properties, PNR, and AOB and AOA abundance. Bold values indicate a significant difference at $P < 0.05$. T_e = elevated temperature alone, C_eT_e = elevated CO_2 and elevated temperature. NH_4^+ = ammonium, NO_3^- = nitrate, N = nitrogen, C = carbon, PNR = potential nitrification rate, AOB = ammonia-oxidizing bacteria, AOA = ammonia-oxidizing archaea.

Factors	Soil moisture	pH	NH_4^+	NO_3^-	Total N	Total C	PNR	AOB abundance	AOA abundance
T_e	**0.001**	0.31	0.52	0.12	0.45	0.593	0.063	0.054	**0.023**
C_eT_e	0.724	0.262	0.34	<**0.001**	0.32	0.201	**0.005**	**0.004**	**0.003**
Time (T)	<**0.001**	**0.002**	**0.004**	<**0.001**	**0.001**	0.068	<**0.001**	<**0.001**	<**0.001**
$T_e \times T$	0.105	0.08	0.07	0.41	0.074	0.312	0.061	0.087	**0.012**
$C_eT_e \times T$	0.496	0.09	0.21	**0.035**	0.08	0.083	**0.002**	**0.008**	**0.002**

PNR ($r_s = 0.590$, $P < 0.001$ and $r_s = 0.685$, $P < 0.001$, respectively, Table 2). Soil total C was also significantly negatively correlated with PNR and ammonia-oxidizer abundance ($r_s = -0.327$, $P = 0.031$; $r_s = -0.413$, $P = 0.022$; $r_s = -0.502$, $P = 0.018$). There were significant correlations between PNR and AOB, AOA community structure (Table 3). The results suggested AOB community were more strongly linked to PNR than AOA community.

4. Discussion

Our results show that nitrification rates and ammonia-oxidizer community structure and abundance in response to climate treatments depended on plant growth stage. In particular, nitrification rate and ammonia-oxidizers responded to climate treatments when plants reached the early flowering stage (70 DAP). C_aT_e did not significantly change potential nitrification rates, but increased AOA abundance and changed AOA community structure, while an increase in nitrification rates and shifts in AOB and AOA abundance and structure under C_eT_e treatments were observed. The abundance and community structure of AOB and AOA were positively correlated with nitrification rates. Overall, our findings highlight the significant positive effects of combined elevated CO_2 and temperature on nitrification kinetics and ammonia-oxidizing communities, thereby increasing soil N availability and subsequent cotton crop productivity, but also indicate loss of N to ground water and atmosphere.

4.1. Effects of elevated temperature alone and in combination with elevated CO_2 on soil physicochemical properties, PNR, and AOB and AOA communities

The C_aT_e treatment did not affect soil physicochemical properties (except soil moisture). AOB community and PNR were not impacted

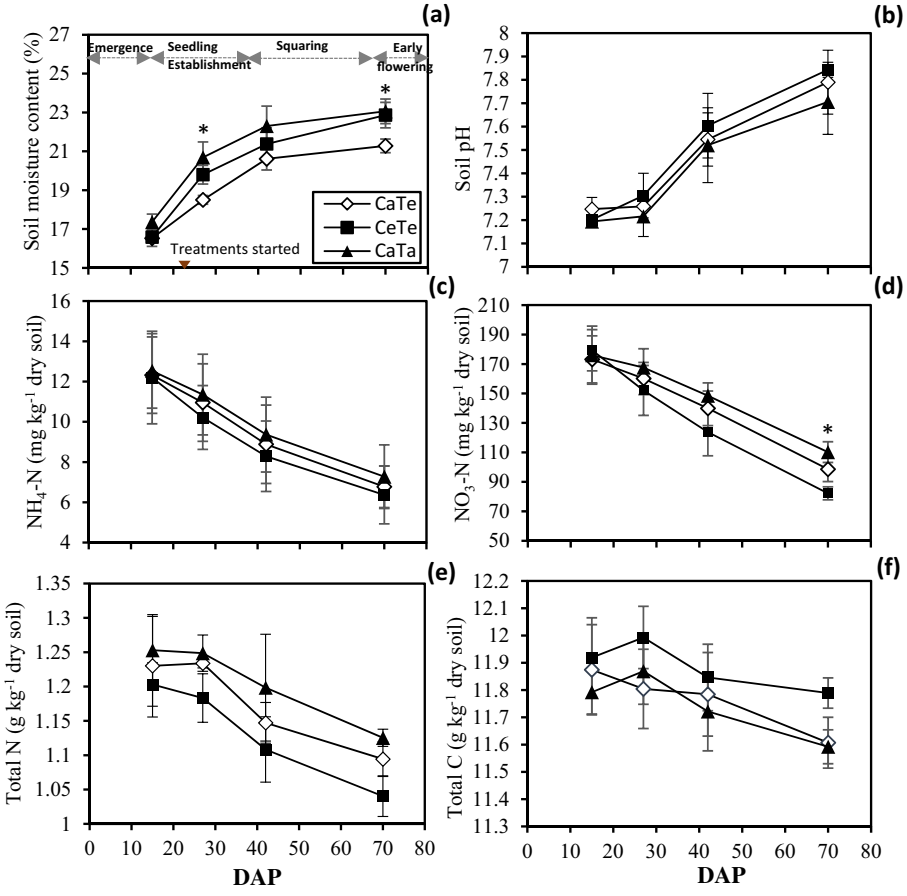

Fig. 2. Changes in soil physicochemical properties under climate treatments during the experiment: (a) Soil moisture, (b) soil pH, (c) soil NH_4^+, (d) soil NO_3^-, (e) soil total N, and (f) soil total C. The asterisk indicates significant difference between different treatments ($P < 0.05$). Values represent mean ± SE ($n = 10$) of each treatment. C_aT_a = ambient CO_2 and temperature, C_aT_e = ambient CO_2 and elevated temperature, C_eT_e = elevated CO_2 and elevated temperature. DAP = day after planting. NH_4^+ = ammonium, NO_3^- = nitrate, N = nitrogen, C = carbon, SE = standard error.

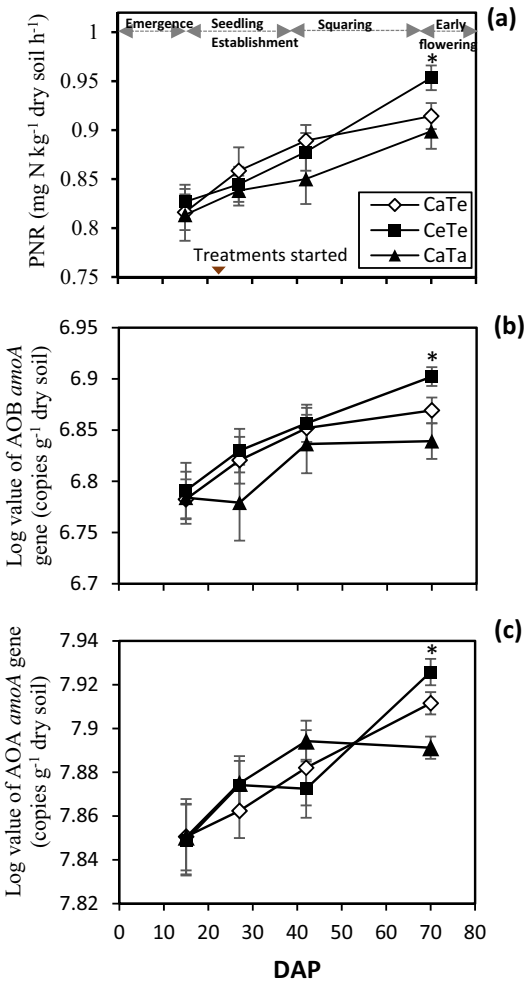

Fig. 3. Changes in (a) PNR, (b) AOB and (c) AOA *amoA* gene abundance under climate treatments during the experiment. The asterisk indicates significant difference between different treatments ($P < 0.05$). Values represent mean ± SE ($n = 10$) of each treatment. C_aT_a = ambient CO_2 and temperature, C_aT_e = ambient CO_2 and elevated temperature, C_eT_e = elevated CO_2 and elevated temperature. AOB = ammonia-oxidizing bacteria, AOA = ammonia-oxidizing archaea, SE = standard error.

by C_aT_e whereas there was an increase in AOA abundance (+4.9%) and shifts in AOA community structure at the early flowering stage. The results contrasted with our hypothesis that C_aT_e would stimulate soil N processes and microbes. These results can be explained by minimal changes (2%) in soil moisture, which is a key factor affecting soil nutrient availability and microbial communities in various ecosystems, between the treatments (Gleeson et al., 2010; Barnard et al., 2013; Hu et al., 2015). These relatively small changes in soil moisture could be due to small differences in air temperature (1.1 °C) between the C_aT_e and C_aT_a plots. In addition, lower VPD (−9%) and PAR (−31%) inside chambers compared to ambient plots were a function of high humidity and chamber cover, respectively, which could counteract effects of the higher temperature on soil nitrification and ammonia-oxidizers. Other factors such as soil pH and NH_4^+ are also important for nitrification and nitrifiers (Giles et al., 2012); however, they did not significantly change in response to C_aT_e in our study, and therefore did not influence PNR and ammonia-oxidizers. This might be partly attributed to no change in N mineralization under C_aT_e in the experiment, although increased temperatures have been reported to stimulate organic matter degradation, resulting in increased mineralized N which would benefit both nitrifiers and plant uptake (Zhou et al., 2012; Nie et al., 2013; Frey et al., 2013); however, N mineralization rates were not measured. Previous studies reported warming-stimulated root exudation and litter decomposition (Uselman et al., 2000; Yin et al., 2013), but we did not examine plant litter and root exudation. In this study, we did observe significantly higher cotton plant biomass in C_aT_e compared to C_aT_a (Broughton 2015, pers. comm.).

Interestingly, we found a significant response of AOA community abundance and structure to C_aT_e at the early flowering stage (70 DAP). It suggested AOA response to C_aT_e was partly related to cotton growth. The response of AOA, but not AOB, to C_aT_e in this study could be attributed to physiological adaptation. Studies on enriched and pure AOA strains have indicated higher optimal temperature in AOA compared to AOB. Tourna et al. (2011) and Hatzenpichler et al. (2008) found that the first soil AOA isolate *Nitrososphaera viennensis* and the moderate thermophilic Candidatus *Nitrososphaera gargensis* favour 37 °C and 46 °C for their growth, respectively. In addition, the thermophilic AOA *Nitrosocaldus yellowstonii* can grow at temperatures up to 74 °C (De La Torre et al., 2008). Qin et al. (2014) indicated *Nitrosopumilus maritimus* SCM1, a marine AOA isolate, performs optimal growth at 32 °C whereas it could not survive at 10 °C. In contrast to AOA, AOB have not shown the ability to survive above 40 °C (Jiang and Bakken, 1999; Hatzenpichler et al., 2008). Thus, approximately 1.1 °C warmer in our study likely stimulated a fraction of AOA which may prefer relatively higher temperatures for their growth. This conclusion was also supported by our finding of increased relative abundance of a dominant AOA TRF-54, which belonged to the *Nitrosopumilus* cluster, under warming conditions.

Although the AOA community significantly responded to C_aT_e, PNR did not significantly change. This could be explained by changes in the less active or dormant fraction, thereby resulting in little difference to overall nitrification kinetics. Our findings contrasted with the study by Hu et al. (2016) which found a strong effect of C_aT_e on nitrification rate and AOA community in natural dryland soils. Nitrification significantly increased in response to 3 °C climate warming due to shifts in AOA community structure and abundance, and stimulation of AOA metabolic activities (Hu et al., 2016). These contradictory results suggest that the response of nitrification to C_aT_e may be ecosystem-specific and could be influenced by management practices, including irrigation and fertilizer application.

The C_eT_e treatment significantly decreased soil NO_3^-, which could be due to enhanced plant uptake, N immobilization or N loss to ground water and atmosphere (Lukac et al., 2010; Luo et al., 2004). Similar trends were observed between soil NO_3^- and cotton biomass in fully factorial experiments conducted in the glasshouse, as well as strong correlations between nitrate depletion in C_e and T_e treatments in relationship to vegetative growth and yield (Osanai et al., 2017a, 2017b). In addition, both AOB and AOA communities positively responded to C_eT_e when cotton plants reached the early flowering stage, resulting in an increase in the rate of nitrification which is directly related to crop yields. The significant increase in AOB and AOA abundance, as well as shifts in their community structure, in response to C_eT_e could be attributed to CO_2-induced plant properties. The responses of soil microbial communities to elevated CO_2 concentrations are mainly due to changes in plant residue inputs and root exudates (Singh et al., 2010). Elevated CO_2 has been demonstrated to increase C assimilation, thereby enhancing plant biomass (Ainsworth and Long, 2005). Cotton plant biomass under C_eT_e has increased significantly (Broughton 2015, pers. comm.), potentially resulting in an increase in root exudates and rhizodeposition which can stimulate soil microbial communities (Rakshit et al., 2012; Jin et al., 2014). Our results are similar to those in a rice field study by Liu et al. (2015), in which elevated CO_2 (500 ppm) alone and in combination with elevated temperature had significant effects on AOB and AOA communities, and PNR possibly due to increased flux of rhizodeposition, root exudates, and secretions in the soil; similarly, these factors were proposed to explain stimulated nitrification under elevated CO_2 in grassland soil studies (Zak et al., 1993; Carnol et al., 2002; Brown et al., 2012). However, a few studies on the effect of CO_2 fertilization on ammonia-oxidizers in agricultural soils have reported opposite results. Elevated

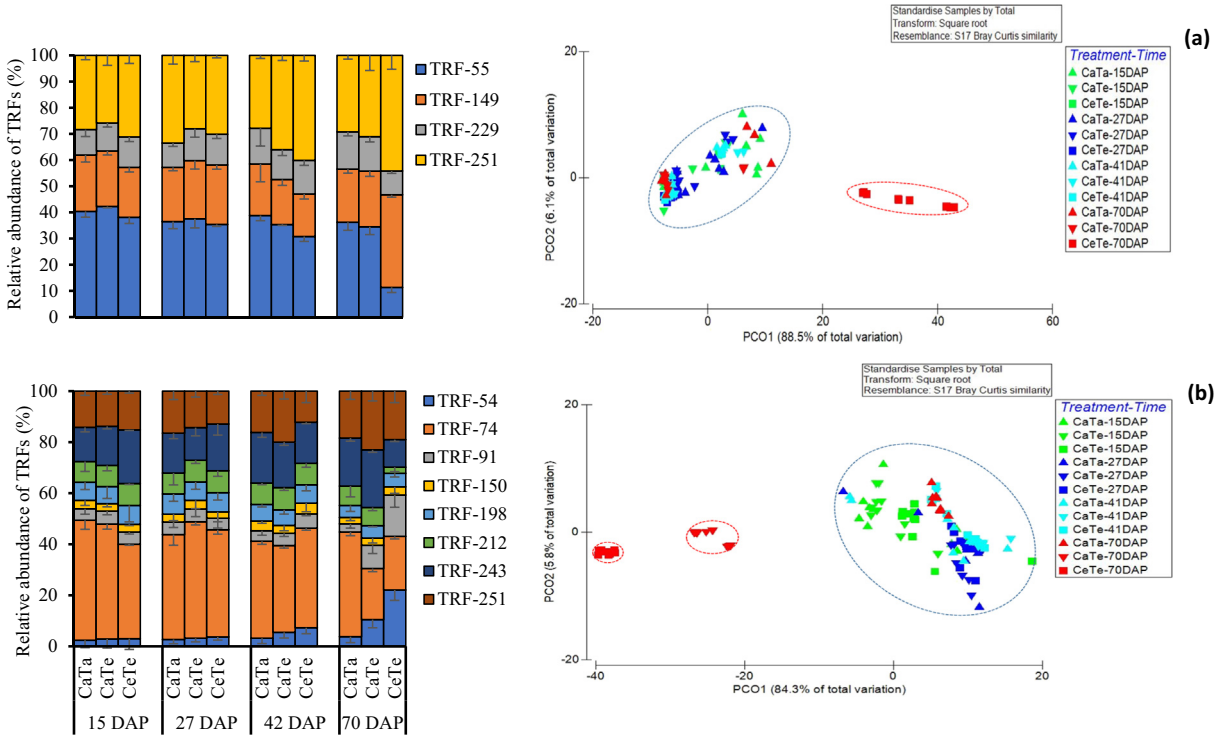

Fig. 4. TRFLP fingerprints and PCO derived from the Bray-Curtis dissimilarity matrices showing differences in (a) AOB and (b) AOA community under climate treatments at different developmental stages including emergence (15 DAP), seedling establishment (27 DAP), the early squaring stage (41 DAP) and early flowering stage (70 DAP). C_aT_a = ambient CO_2 and temperature, C_aT_e = ambient CO_2 and elevated temperature, and C_eT_e = elevated CO_2 and elevated temperature, DAP = day after planting, AOB = ammonia-oxidizing bacteria, AOA = ammonia-oxidizing archaea.

CO_2 had no significant effect on AOA and AOB abundance in the rhizosphere of maize and soybean (Nelson et al. (2010)) and the soybean FACE experiment observed no significant effects of elevated CO_2 on nitrifying communities (Pereira et al., 2011). These studies suggested that no effect of elevated CO_2 on nitrification were due to the enhancement of N immobilization as a function of potential increases in soil C/N ratio; therefore, the climate effect on nitrifying communities may be dependent on crop type, soil type, management practices and climatic conditions.

4.2. The relationship between PNR and ammonia-oxidizing communities

The abundance of AOA is higher than AOB in various terrestrial ecosystems (Hu et al., 2015; Yao et al., 2013). Similarly, the abundance of AOA was approximately 10-fold higher than AOB in our study. Both AOB and AOA were significantly correlated with PNR, suggesting that nitrification rate was driven by both AOB and AOA in irrigated cotton under future climate. However, AOB community was more strongly correlated with PNR than AOA community. This finding gives more insights into the relationship between microbial communities and their functioning. Our results are similar to Di et al. (2009) and Banning et al. (2015) who reported the stronger functional extent of AOB than their counterpart AOA in nutrient-rich soils. These results might have been observed because cotton farming systems are often well-watered and receive a large amount of N fertilizer, thereby favouring the AOB community. In contrast, AOA become functionally dominant in harsh environments, such as nutrient-poor drylands, due to their advantages over AOB because of their high substrate affinity and oligotrophic life history (Yao et al., 2013; Hu et al., 2016).

Table 2
Spearman correlation coefficients of soil physicochemical properties, PNR and the abundance of AOB and AOA communities. Significant correlations at $P < 0.01$ (**) and $P < 0.05$ (*) are in bold. PNR = potential nitrification rate, AOB = ammonia-oxidizing bacteria, AOA = ammonia-oxidizing archaea, NH_4^+ = ammonium, NO_3^- = nitrate, Total C = total carbon, Total N = total nitrogen.

Variables	Soil moisture	pH	NH_4^+	NO_3^-	Total C	Total N	PNR
AOA	0.179	0.359	−0.326	−0.353	**−0.502***	−0.323	**0.507***
AOB	0.266	**0.590****	−0.266	−0.267	**−0.413***	−0.421	**0.81****
PNR	0.321	**0.685****	−0.467	−0.127	**−0.327***	−0.265	–

5. Conclusions

Our results indicated that the moderate 1.1 °C warming had no significant effects on soil properties, PNR and AOB community in field conditions. However, AOA community structure and abundance were significantly and positively responsive to C_aT_e. In contrast, soil NO_3^- decreased, while PNR, AOB and AOA abundance increased and shifts

Table 3
The variation explained, the Spearman rank correlation coefficient (r_s), and the P values of correlations between PNR, and (a & b) AOB and AOA community structures, as summarized by the top two principal coordinates (PCO1 & PCO2). Significant effects are in bold ($P < 0.05$). AOB = ammonia-oxidizing bacteria, AOA = ammonia-oxidizing archaea, PNR = potential nitrification rate.

Statistic	PCO1	PCO2
(a) AOB		
Variation explained (%)	88.5	6.1
PNR		
r_s	**−0.511**	**−0.288**
P	**<0.001**	**0.001**
(b) AOA		
Variation explained (%)	84.29	5.84
PNR		
r_s	**−0.43**	−0.148
P	**0.001**	0.106

in ammonia-oxidizing community structure occurred in response to C_eT_e treatment. Climate responses of soil physicochemical properties, nitrification rate and ammonia-oxidizers were related to cotton growth stages. These changes in functional communities and the rate of nitrification could potentially alter soil N availability, which is directly related to crop productivity and environmental quality. Although our field observations were supported by previous glasshouse experiments (Osanai et al., 2017a, 2017b), it should be noted that we did not have a full factorial experimental design and were limited by the number of chambers in each treatment and the relatively short duration of the experiment. Nonetheless, our findings provide novel insight into short-term effects of climate change on the relationship between microbial communities and their function, which may be similarly affected in the long-term but need to be tested in future experiments. Hence, this should provide greater capacity to predict the response of agroecosystems, particularly N-dependent cotton crop systems, to combined elevated CO_2 and temperature, and allow us to develop more effective N management strategies in future climates.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.04.181.

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